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Consequences of extreme events on population persistence and evolution of a quantitative trait

Simone Vincenzi [a,b,*], Giulio A. De Leo [c,d], Michele Bellingeri [c]

[a] Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, United States
[b] MRAG Americas, POB 1410 Capitola, California 95010, United States
[c] Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Viale G. P. Usberti 33/A, I-43100 Parma, Italy
[d] Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 United States

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ABSTRACT

The intensification and increased frequency of weather and climate extremes are emerging as one of the most important aspects of climate change. Using a quantitative genetic model, we explore the effects of increasing environmental stochasticity and its interplay with genetic variation and selection pressure on population dynamics and evolution of a fitness-related trait. We use simulations with variations in trend (i.e., directional change) and stochasticity (i.e., increase in variance) of a climate variable defining a phenotypic optimum, and various hypotheses on mutational variance and strength of selection on a phenotypic trait. We let the population reach mutation–selection balance and then we linearly increase over simulation time both the mean and the variance of the statistical distribution of the climate variable. Higher variance of climate variables increases the probability of extreme climatic events, i.e. events that are both statistically rare and with potentially high ecological impact, that is, causing episodes of massive mortality in the population.

Our analysis shows that the population is able to track the directional component of the optimum for low increases of variability, while for high increases the tracking is reduced. Persistence of the population depends quite strongly on the selection pressure and decreases with increasing variance of the climate variable. Higher mutational variance does not substantially decrease the risk of extinction of a population.

1. Introduction

With climate change, many species will experience selection pressures in new directions and at new intensities, and the degree to which species respond adaptively will have an important influence on their capacity to survive over the coming decades and millennia. Changes in the long-term mean state of climate variables (i.e., climate trends) and their consequences on survival, evolution and adaptation of species have been intensively studied for more than 20 years (Hoffmann and Sgrò, 2011), and a wealth of quantitative genetic studies on the effects of environmental change on population persistence and evolution of traits under selection has been published. Burger and Krall (2004) grouped environmental changes according to their temporal occurrence: stochastic fluctuations of a certain parameter around a constant mean; periodic fluctuations around a constant mean which are at least partially predictable; directional changes, such as global climatic changes, and abrupt change in the environment.

We now describe some of the most relevant results and insights from quantitative genetic studies relevant to environmental and climate change. Lynch and Lande (1993) and Bürger and Lynch (1995, 1997) investigated the extinction dynamics of a population when the optimum moves at a constant rate per generation. They found a critical rate of environmental change beyond which extinction is certain because the lag (difference between the mean trait in the population defining fitness and the optimum for that trait) increases from generation to generation, thus decreasing the mean fitness of the population below a level at which the population starts to decline. With a smaller population size, genetic drift reduces the genetic variance, which leads to an even larger lag, a further decrease of mean fitness, and rapid extinction.

In many systems, changes in environmental factors, and thus selection, are both directional (e.g., higher temperatures, higher rainfall) and fluctuating (e.g., through cycles, stochastically). In addition, climate change models show that the variance of climate variables such as temperature or rainfall may change much more dramatically than their means (e.g., Kharin and Zwiers, 2000) and will thus intensify the stochastic component of selection. Charlesworth (1993) and Lande and Shannon (1996) investigated fluctuating stabilizing selection on a quantitative trait by assuming that the optimum phenotype follows a linear stationary Markov process with autocorrelation

* Corresponding author at: Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, United States.
E-mail address: simon.vincenz@gmail.com (S. Vincenzi).

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between −1 and 1. They showed that genetic variation is only beneficial if the variance of the fluctuations is high or if the process is highly autocorrelated, in which case adaptation, that is tracking the optimum, increases the mean fitness. On the contrary, with uncorrelated environmental noise, an increase in genetic variation always causes a decrease in mean fitness. Bürger (1999) found that when environmental variability is high, a high reproductive rate is much more effective at improving population persistence than a high genetic variance.

Individual-based quantitative genetic models with stochastic dynamics (Gomulkiewicz and Holt, 1995; Holt and Gomulkiewicz, 2004) suggest that evolution may quickly rescue populations after they collapse under abrupt environmental change. Fitness is predicted to initially decline after the abrupt change, but then recover through adaptation (e.g., Burt, 1995). According to such theory, whether populations can be rescued through evolution of fitness-related traits depends upon several crucial variables, including population size, genetic variation within the population, and the degree of maladaptation to the new environment (Bell and Gonzalez, 2009).

Shifts and excursions in climate or environmental variables might cause some populations to perpetually chase alternate optimal phenotypic extremes. Such populations would face a demographic cost if evolution during one environmental phase resulted in maladaptation and reduced favorable genetic variation with respect to the next.

While it is well known that small populations are usually highly vulnerable (i.e., are at high risk of extinction) to even moderate environmental stochasticity, the picture emerging from quantitative genetic studies of population dynamics shows that large populations can also be vulnerable if the environmental variability is sufficiently high.

The intensification of weather (individuals events, such as hurricanes) and climate (events over seasons, such as droughts) extremes is emerging as one of the most important aspects of climate change (Jentsch et al., 2007) and the debate is expanding from an analysis of trends to an interest in extreme events. Weather and climate extremes are characterized by intensity, duration, frequency, or spatial extent; they can disrupt ecosystems, communities, or population structure and change resource pools, substrate availability, or physical environment (Jentsch et al., 2007; Wagner, 2003; White et al., 1985). Many adaptations (in life histories, morphological or behavioral traits) are associated with extreme events (Stockwell et al., 2003).

It is well known that populations can survive a single extreme event, especially if short-lived, and rapidly recover through various compensatory responses (e.g., Spiller et al., 1998; Wingfield et al., 2011). Under scenarios of climate change it is possible that a population may experience a long sequence of particularly extreme climatic events capable of driving the population to extinction (Jentsch et al., 2007). In addition, even when extinction does not immediately follow an extreme event, the loss of genetic variability resulting from the dramatic drop of population size to very low densities can substantially reduce the population's ability to respond to future selective challenges and increases the chances of an extinction vortex (e.g. Caughley, 1994).

There is growing evidence that the frequency and severity of weather and climate extremes and associated ecological responses have already increased in several regions (Karl et al., 2005; Schär et al., 2004). These events may result in rapid mortality of individuals and extinction of populations or species (Bigler et al., 2006, 2007; Gitlin et al., 2006; Miriti et al., 2007; Thibault and Brown, 2008) and changes in community structure and ecosystem function (Ciais et al., 2005; Haddad et al., 2002; Mueller et al., 2005).

Hence, there is the urgent research need to meet the challenges posed by extreme events. However, in the context of quantitative genetic models, the joint effect of a directional change and of a large increase in variance of a climatic variable leading to higher occurrence of extreme events, as expected under scenarios of climate change (IPCC, 2007), has scarcely been investigated.

Here, we use a simple quantitative genetic model to explore the evolution of a fitness-related trait in a population and its effects on population dynamics with a gradual increase in mean and variance of a climate variable determining the optimum for the trait under selection. We perform the analysis with alternative assumptions on strength of the selection pressure, mutation, and on the rate of directional change and increase in climate variability.

2. Model of population dynamics

2.1. General description of the model

We consider a population of hermaphrodite individuals living in a habitat with carrying capacity K, here intended as the maximum number of individuals supported. This allows us not to keep track of males and females and introduces density-dependent population regulation through a ceiling effect, as described below.

The population has discrete generations (i.e., reproduction is discrete in time) and is composed of N(t) individuals. Generations are overlapping, meaning that parents do not die after reproducing. Each individual is characterized by a single quantitative trait a corresponding to its breeding value for a phenotypic trait z. The habitat is characterized by an optimum phenotype Θ that changes over time as a result of variations in a climate driver, such as rainfall or temperature, selecting for the phenotypic trait z. The distance between the optimum phenotype $\Theta(t)$ and the trait z of the i individual z_i defines the maladaptation of an individual, as described in detail in the following. The time step is one year.

2.2. Temporal change of optimum phenotype

In general, the temporal change of the optimum phenotype Θ may be either directional, stochastic or a combination of both. A simple model for this is an optimum phenotype $\Theta(t)$ that moves at a constant rate $\beta_{\mu,\ \Theta}$ over time, fluctuating randomly about its expected value $\mu_\Theta(t)$. We thus introduce a directional and stochastic temporal change of the optimum phenotype (Fig. 1a). $\Theta(t)$ is randomly drawn at each time step from a normal distribution $\Theta(t) \sim N(\mu_\Theta(t), \sigma_\Theta(t))$:

$$\begin{cases} \mu_\Theta = \mu_{\Theta,\ 0} & for\ t<t_{ch} \\ \sigma_\Theta = \sigma_{\Theta,\ 0} & \\ & \\ \mu_\Theta(t) = \mu_{\Theta,\ 0} + \beta_{\mu,\ \Theta} t_{ch} & for\ t>t_{ch} \\ \sigma_\Theta(t) = \sigma_{\Theta,\ 0} + \beta_{\sigma,\ \Theta} t_{ch} & \end{cases} \quad (1)$$

where t_{ch} is the time since the change in the environment. The definition of extreme events in ecological models is a thorny question. First, while for weather extremes the definition is more straightforward (e.g., a hurricane may always be considered an extreme event), what constitutes a climate extreme strongly depends on the available climate record. In the following, our considerations will be based on climate extremes, e.g., exceptionally high temperatures leading to a drought or rainfall over a season leading to repeated floodings.

A climate extreme for a particular environmental parameter can be readily represented by the distribution of the set of largest values recorded in a time window or, equivalently, by the tails of a probability distribution of a climate variable, whose shape and parameters have been estimated on historical series of observations. Both tails are relevant, since both extremely high and low temperatures or rainfall (potentially causing droughts and floods, respectively) have potentially extreme consequences. Second, a climate extreme is not always driving an extreme ecological response. In fact, depending on the role and abundance of the species impacted, such responses may or may not result in changes that can be distinguished from background variability (Smith, 2011).